Coral species composition drives key ecosystem function on coral reefs

Richardson, Laura; Graham, Nicholas A.J.; Hoey, Andrew

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Title

Coral species composition drives key ecosystem function on coral reefs

Authors

Laura E. Richardson [1,2] *l.richardson@bangor.ac.uk

Nicholas A. J. Graham [1,3]

Andrew S. Hoey [1]

[1] ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia.

[2] School of Ocean Sciences, Bangor University, Menai Bridge, LL59 5AB, United Kingdom.

[3] Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, United Kingdom.

*Corresponding author

Abstract

Rapid and unprecedented ecological change threatens the functioning and stability of ecosystems. On coral reefs, global climate change and local stressors are reducing and reorganising habitat-forming corals and associated species, with largely unknown implications for critical ecosystem functions such as herbivory. Herbivory mediates coral-algal competition, thereby facilitating ecosystem recovery following disturbance such as coral bleaching events or large storms. However, relationships between coral species composition, the distribution of herbivorous fishes, and the delivery of their functional impact are not well understood. Here, we investigate how herbivorous fish assemblages and delivery of two distinct herbivory processes, grazing and browsing, differ among three taxonomically distinct, replicated coral habitats. While grazing on algal turf assemblages was insensitive to different coral configurations, browsing on the macroalga *Laurencia* cf. *obtusa* varied considerably among habitats, suggesting that different mechanisms may shape these processes. Variation in browsing among habitats was best predicted by the composition and structural complexity of benthic assemblages (in particular the cover and composition of corals, but not macroalgal cover), and was poorly reflected by visual estimates of browser biomass. Surprisingly, the lowest browsing rates were recorded in the most structurally complex habitat, with the greatest cover of coral (branching *Porites* habitat). While the mechanism for the variation in browsing is not clear, it may be related to scale-dependent effects of habitat structure on visual occlusion inhibiting foraging activity by browsing fishes, or the relative availability of alternate dietary resources. Our results suggest that maintained functionality may vary among distinct and emerging coral reef configurations due to ecological interactions between reef fishes and their environment determining habitat selection.

Keywords

Species composition; ecosystem function; habitat selection; herbivory processes; community structure; climate change

Introduction

Global climate change and mounting local stressors are degrading ecosystems via species extirpations and introductions, modifying the composition of assemblages and threatening ecological function [1,2]. Non-random species turnover, ordered by the susceptibility of organism traits [3], is increasing the taxonomic and functional similarity of communities [4-6]. These changes can disrupt ecosystem processes, such as habitat provisioning [7,8], primary productivity [9], trophic energy flow [10], nutrient cycling [11,12], and pollination [13]. Whilst evidence exposes a coherent pattern of ecological change across biomes [14], variation exists from the individual to community level in how ecological structure, ecosystem processes, and ongoing disturbance dynamics interact [15,16]. For effective and adaptive local management, better understanding is needed of the extent to which different, and in some cases emerging, species configurations support processes critical to ecological stability [17].

We focus on coral reefs, one of the most biodiverse but threatened ecosystems [18], to elucidate how the composition of habitat-building species (i.e. corals) influences key ecosystem functions. Climatic changes and local human impacts have reduced populations of corals, resulting in unprecedented loss of coral cover and marked shifts in coral species composition due to differential susceptibilities of corals to thermal stress, severe storms, predation by crown-of-thorns starfish, and poor water quality [19,20]. Typically stress-sensitive, topographically complex branching corals (e.g. Acroporidae) are replaced by more robust, prostrate corals (e.g. Mussidae, Poritidae) following disturbance [20,21]. The composition and cover of coral species are key determinants of the structural complexity of reef habitats [21,22], and can exert considerable influence over the taxonomic and functional

structure of reef fish assemblages [6]. However, the capacity of altered coral species configurations to support key ecosystem processes despite on-going disturbance is largely unknown and of growing concern [20,23].

Herbivory, the consumption of algal material, is dominated by fishes on coral reefs with relatively intact fish assemblages. Herbivory processes can promote coral dominance by reducing the cover and/or biomass of algae, though the amount of herbivory necessary will depend on the extent of substrate available to algae, background nutrient levels that can accelerate algal increase [24], and the effect of anthropogenic ocean warming on corals [25]. If herbivory is sufficient, it can mediate competitive interactions with corals [26], mitigate shifts to macroalgal dominance following extensive coral mortality, and facilitate recovery of coral populations [27]. However, the distribution of herbivorous fishes and their rates of herbivory can be highly spatially variable; among regions [28,29], latitudes [30], across the continental shelf [31], with the amount of nutrients entering the system [32], and among reef zones [33,34]. Importantly, rates of herbivory by fishes often vary among sites within reef zones [35,36], with studies relating variation to differences in habitat structural complexity [28], the cover of live coral [29,37], the relative palatability of resident algal communities [34,38], predation pressure, or competition for resources [39]. Where variation in herbivory is driven by the differential composition of benthic reef habitats [35], this may carry implications for the variable functioning of distinct coral species configurations. However, relationships between coral species composition and herbivory processes by fishes at the within-reef scale remain unclear.

Herbivory processes are diverse, carried out by multiple species that perform complementary, and in some cases functionally overlapping, roles in removing algae from the reef substrate

[40,41]. For example, grazing fishes (including algal croppers/detritivores, scrapers, and excavators) feed on surfaces covered by epilithic algal matrices (EAM: a conglomerate of algal turfs, macroalgal propagules, sediment, detritus and microbes; [42]), but have limited capacity to remove large fleshy macroalgae [38]. By feeding on EAM covered surfaces, grazers maintain algal communities in a cropped state, reduce the growth of macroalgal propagules within the EAM, reduce coral-algal competition and thereby facilitate settlement, growth and survival of corals and coralline algae [41]. In contrast, macroalgal browsers typically feed on larger fleshy macroalgae and have the potential to reverse phase shifts by removing macroalgae biomass, facilitating the recovery of coral populations [27,43]. Understanding the extent to which different configurations of structurally distinct corals maintain populations of herbivorous fishes and the critical functions they provide, is paramount for the management of ecological integrity yet is largely unknown.

The primary objective of this study was to investigate how grazing and browsing herbivory processes by reef fishes varied among coral habitats that differed in coral species composition and structural complexity across within-reef scales [22]. Using a combination of *in situ* surveys and transplanted algal assays across three replicated habitats characterised by the predominance of distinct coral taxa (*sensu* [22]), we specifically ask the following questions: 1) Do the structure of herbivorous fish assemblages and rates of grazing and browsing vary among reefs characterised by distinct coral habitats? 2) What is the relative influence of coral species composition and structural complexity, and herbivore biomass on these herbivory functions within reefs?

Methods

Study sites

This study was conducted in April and May 2016 on coral reefs surrounding the continental high islands of the Lizard Island Group, 33 km off the mainland coast of Cape Flattery in the northern Great Barrier Reef (14°41′S, 145°27′E; Fig. S1). Three replicate sites of three taxonomically and structurally distinct coral habitats were selected on shallow (<6 m) reefs, based on surveys completed in September 2015 [22]. These three habitats were characterised by predominant cover of: i) branching *Porites* (mostly *P. cylindrica*); ii) soft coral (mostly *Lobophyton*, *Sarcophyton*, and *Sinularia*); and iii) mixed coral assemblages (mostly staghorn, corymbose and plating *Acropora*, massive and branching *Porites*, *Lobophyton*, *Sarcophyton*) (Fig. S2; Table S2). The study coincided with a large-scale coral-bleaching event at Lizard Island [44], with fish and benthic communities affected across the study sites [6]. At each site, we quantified herbivore fish and benthic assemblages (including extent of coral bleaching), and the consumption of algal turfs and a locally abundant macroalga. All sites (each >250 m x 5 m) were positioned on the leeward side of the islands protected from the prevailing south-east swell, had comparable geomorphology and water clarity [45,46], and were separated by >500 m.

Benthic composition and herbivore assemblages

Benthic composition was quantified along six 30 m point-intercept transects at each site, recording the substratum immediately under the tape every 25 cm (120 points per transect). Transects were positioned approximately 2.5 m from, and parallel to, the reef-sand interface. Substratum categories were hard (scleractinian) corals identified to genus (or species where possible) and morphology, soft (alcyonacean) corals identified to genus, ‘other sessile

144 invertebrates' (mainly clams, sponges, and ascidians), macroalgae identified to genus, 'dead
145 substrata' (dead coral and pavement, covered in EAM), rubble, and sand. For corals directly
146 under surveyed points, the extent of bleaching was assessed *in situ* using the CoralWatch
147 colour reference card estimating coral tissue colour saturation on a 6-point scale (1-2
148 considered 'bleached').
149
150 To account for behavioural plasticity, functional overlap, and uncertainty regarding specific
151 herbivore species particularly across their different life history stages [40,43,47], the
152 abundance and total length (TL; nearest cm) of all nominally herbivorous fishes (i.e.
153 Acanthuridae, Kyphosidae, Pomacanthidae, Scarinae, Siganidae, Pomacentridae; Table S1)
154 were visually censused along the same six 30-m transects used to quantify benthic
155 assemblages. Omnivorous herbivores known to consume algae in addition to zoobenthos and
156 zooplankton were also censused. Fishes >10 cm TL were recorded within a 5-m wide belt
157 while initially deploying the transect tape to minimise disturbance to fish assemblages, and
158 those ≤10 cm TL were recorded within a 1-m wide belt on the return swim. Fish abundance
159 estimates were standardised per 150 m^2 and converted to biomass (kg ha^{-1}) using published
160 species length-weight relationships (Table S1). All surveyed species were categorised into six
161 nominal groups (i.e., macroalgal browsers, croppers/detritivores, scrapers, excavators,
162 farmers, and omnivorous herbivores) based on their diet and feeding behaviour (Table S1).
163
164 *Rates of herbivory*
165
166 To quantify rates of grazing on algal turfs among habitats, we exposed established turf algal
167 communities on terracotta tiles (10 x 10 x 1 cm) with to resident herbivores at each site for
168 seven days. To establish turf algal communities, 79 tiles were deployed at a single shallow

169 reef site (~2 m depth) at Lizard Island, covered with plastic mesh (5 cm square mesh) to
170 exclude feeding by large herbivorous fishes and left *in situ* for six months. After this period,
171 the tiles were collected, and eight haphazardly selected tiles were deployed at each of the nice
172 sites. Six tiles were exposed to local herbivores, and two were placed inside individual
173 exclusion cages (300 x 300 x 300 mm; 12-mm^2 steel mesh) to determine if observed changes
174 in algal turf height were due to herbivory (cages: at each site. An additional caged tile was
175 included at seven of the nine sites (all sites except one mixed coral site and one soft coral
176 site). The tiles were deployed at each site by securing to individual cement pavers with a
177 galvanized steel nut and bolt through the centre of the tile. The pavers were placed on
178 horizontal surfaces that were free of live coral at each site, with >10 m between adjacent
179 pavers/tiles. Exclusion cages were cleaned of fouling organisms (mostly algae) every two to
180 three days. The initial height of the turf algal community was quantified at nine uniformly
181 spaced points *in situ* using callipers (nearest mm) across the upper surface of the tile
182 immediately after deployment (mean ± SE = 4.89 mm ± 0.13; no significant variation among
183 habitats, lme, $F_{2, 6}$=1.14, P=0.38), and again after seven days.
184
185 To quantify rates of macroalgal browsing, transplanted "bioassays" (hereafter 'assays') of the
186 red macroalga *Laurencia* cf. *obtusa* were used. *Laurencia* was selected as it was the most
187 abundant macroalga on reefs surrounding Lizard Island at the time of the study, and
188 *Laurencia* spp are known to be consumed by herbivorous reef fishes on the Great Barrier
189 Reef [48,49]. Thalli of *Laurencia* were collected by hand from a local shallow reef flat and
190 placed in an aquarium (6000 L) with flow-through seawater within 30 mins of collection.
191 Whole thalli of similar size were spun in a salad-spinner for 30 s to remove excess water, and
192 the wet weight recorded (to the nearest 0.1 g). The initial mass (mean ± SE) of each assay
193 was 45.4 ± 1.0 g. Six haphazardly selected assays were transplanted to each site between

0930-1030 h, with three exposed to resident herbivore assemblages and three placed within adjacent herbivore exclusion cages (300 x 300 x 300 mm) for 24 h. Each caged assay was positioned within 2 m from its paired exposed assay, and adjacent assay pairs were separated by a minimum of 10 m. Assays were deployed with a short (<10 cm) length of PVC-coated wire (2 mm diameter) around the thallus base and attached to a small lead weight. Small plastic tags placed adjacent to assays were used to identify individual thalli. After 24 h assays were collected, spun and re-weighed. This procedure was replicated on three non-consecutive days at each site (*n*=9 exposed assays per site).

To identify herbivorous fish species removing *Laurencia* biomass, stationary underwater video cameras (GoPro) recorded feeding activity on up to three (mean=2.2 assays) haphazardly selected assays at each site on each day. Each camera was attached to a dive weight (2 kg) and positioned approximately 1 m from each assay, with a scale bar temporarily placed adjacent to each assay at the start of filming to allow calibration of fish sizes on video footage. Filming commenced immediately after assays were deployed and was continuous for 2.2-4.4 h (variable duration due to differences in battery life among cameras). This procedure was replicated on each day of the experiment (3 per site), resulting in 20.5 ± 1.7 h (mean ± SE) of video observations for each site (189 h in total). Body-size (TL) and number of bites taken from the *Laurencia* by each species on the video footage were recorded. To account for variation in fish body-size on algal mass removed per bite, mass-standardised bite impact was calculated as the product of the number of bites and the estimated body mass for each individual (following [50]). Bite impact was then standardised per hour to account for varying video lengths (mass-standardised bites h^{-1}).

Data analysis

Benthic composition and herbivore assemblages

Variation in the total cover of hard and soft coral, bleached coral (hard and soft), macroalgae, and dead substrata and macroalgae combined among habitats was analysed with linear mixed effects models (lme in *nlme*; fixed factor: habitat, random factor: site), with Tukey's multiple comparisons *post hoc* to identify significant differences (*multcomp*).

Variation in taxonomic composition of herbivorous fish assemblages among habitats was visualised with non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis similarities of log-transformed biomass data (kg ha^{-1}; log (x+1)-transformed), and differences assessed with two-factor nested PERMANOVAs (9999 permutations), using habitat (fixed factor) and site (random within habitat), and Monte Carlo pairwise comparisons. Variation in total biomass (kg ha^{-1}) of all herbivores (log-transformed) among habitats was assessed with a linear mixed effects model fitted with Gaussian residual structure (lme in *nlme;* fixed: habitat; random: site). Variation in herbivore species richness (Poisson distribution), total herbivore abundance, and grazer biomass (combined biomass of croppers/detritivores, scrapers, excavators, and omnivorous herbivores; both models using negative binomial distributions) was assessed with generalised mixed models to accommodate non-stable variances and alternative exponential residual distributions (glmer in *lme4*), followed by Tukey's multiple comparisons to identify significant differences among habitats (*multcomp*). Variation in macroalgal browser biomass was assessed using the same fixed and random effects, but with a zero-inflated negative binomial generalized linear mixed effects model (glmmTMB in *glmmTMB*, and multiple comparisons for glmmTMB in https://cran.r-project.org/web/packages/glmmTMB/vignettes/model_evaluation.html#multcomp).

244

245 Rates of herbivory

246

247 Variation in the reduction in height of algal turfs, and reduction in biomass of *Laurencia*
248 assays among habitats was assessed with linear mixed effects models with a Gaussian
249 residual structure (with lme in *nlme*). Models included habitat, treatment (exposed vs caged-
250 control), and their interaction (fixed effects), and site (random effects). Day of deployment
251 was included as an additional random effect for the model of the reduction in *Laurencia*
252 biomass. A generalised mixed effects model with a negative binomial distribution was used
253 to assess variation in feeding on *Laurencia* (total mass-standardised bites h^{-1}) due to
254 exponential residual distribution, with habitat (fixed), site, and day of deployment (random).
255 Multiple linear regression and information-theoretic model selection was used to assess the
256 relative influence of centred site-mean environmental variables on the change in exposed
257 assays (assay loss) where significant differences were found among habitats: the first axis of
258 a principal components analysis of benthic composition (accounting for 61.7% variation in
259 benthic composition of transects among habitats); percent cover of dead substrata and
260 macroalgae; and underwater visual census (UVC) estimated biomass of nominal herbivore
261 groups (grazers or browsers). Total coral cover was collinear with the cover of dead substrata
262 and macroalgae so was not included. All variables had a variance inflation factor (VIF) <2,
263 and multi-model inference (including null models) estimated by ranked changes in AICc <2.

264

265 Model assumptions of homogeneity of variance and normality were validated with visual
266 assessment of Pearson residuals, and multicollinearity of explanatory variables in the multiple
267 linear regression analysis was assessed by calculating relative VIF. Where variance was
268 heterogeneous among habitats, a constant covariance structure was fitted (i.e. change in

macroalgal weight; percentage cover of macroalgae, bleached coral, and hard and soft coral). All analyses were performed in R (R Core Team 2019), and Primer v6 with PERMANOVA+.

Results

Benthic composition and herbivore assemblage structure

Total coral cover was significantly higher in branching *Porites* habitats than mixed coral habitats (contrast 16.6%, confidence interval CI: 27.48 | 5.67) and intermediate in soft coral habitats (Fig.1a; Table S3). There was no significant variation in the total cover of bleached coral or macroalgae among habitats (Table S3), the latter being low across all sites (mean: 0.3-1.4%) and comprised mainly of *Padina*, *Halimeda*, and *Dictyota*. However, the cover of dead substrata and macroalgae (predominately turf algae) was lower in branching *Porites*-than mixed coral habitats (contrast: 17.2%, CI: 3.09 | 31.36) and intermediate in soft coral habitats (Table S3).

The taxonomic composition of herbivorous fish assemblages differed significantly between branching *Porites* habitats and soft coral habitats, largely driven by differences in the relative biomass of grazing species, such as the parrotfishes *Chlorurus microrhinos, Scarus niger, S. rivulatus*, and the surgeonfishes *Acanthurus blochii* and *Ctenochaetus striatus* (PERMANOVA, Pseudo-F=2.47, df=2,53, P=0.004, unique permutations=280; pairwise test, P(MC)=0.004; Fig. 2). Herbivore assemblages from the mixed coral habitat did not differ from the other two habitats. Variation in herbivore assemblages (species richness, total biomass, biomass of grazers, and browsers) among habitats was inconsistent with the cover

of turf and macroalgae described above. Herbivore species richness and total herbivore biomass (kg ha^{-1}; log-transformed) were significantly greater in mixed coral habitats than soft coral habitats, and intermediate in branching *Porites* habitats (Fig. 1b and c; Tables S3 and S4) as was the biomass of grazers (Table S5). Conversely, the biomass of browsers was significantly greater in branching *Porites* habitats than soft coral habitats (CI: 1.43 | 11.98), and intermediate in mixed coral habitats (Fig. 3; Tables S4 and S5).

Rates of herbivory

Although the reduction in height of algal turf assays differed among habitats (both caged and exposed), with the greatest reduction in the soft coral habitat and lowest reduction in the branching *Porites* habitat, the difference between caged and exposed tiles (i.e. the reduction in height due to herbivores) was consistent among habitats (Fig. 4a; Table S6). The reduction in algal turf height on tiles exposed to local herbivore assemblages was significantly greater than on caged tiles across all habitats (CI: 0.21 | 1.38).

The reduction in *Laurencia* biomass was greater in the mixed coral and soft coral habitats than in the branching *Porites* habitats where the change in weight of exposed assays did not differ significantly to caged assays (Fig. 4b; Table S6). Model selection of variables that explained the reduction in mass of *Laurencia* assays yielded two models within $\Delta AICc<2$ of the top model (Table S7). The most parsimonious included the cover of dead substrata and macroalgae (relative importance: 1.00) and first axis of the principal component of benthic composition among habitats (PC1; relative importance: 0.53), and was 1.1 times more plausible than the second ranked model (Table S7). Across both top models, dead substrata

and macroalgae had a significant (CI: 0.04 | 0.98) and positive effect on assay weight change, whilst PC1 did not have a significant effect (CI: -1.76 | 0.29) (Table S7).

Total feeding on *Laurencia* assays was significantly lower in the branching *Porites* habitat than mixed coral habitat (CI: 3.32 | 3347.43), and intermediate in the soft coral habitat (Fig. 4; Table S6). Analysis of video footage revealed 35 species of reef fishes taking bites from exposed assays across all habitats, with four species accounting for 96% of total mass-standardised bites: *Naso brevirostris* (69%), *Siganus doliatus* (13%), *N. vlamingii* (9%), and *Pomacanthus sexstriatus* (6%). Feeding by each of these species was highly variable among assays and sites, and poorly reflected UVC estimates of fish biomass (Fig. S3). Of these four species, only *P. sexstriatus* was recorded feeding in branching *Porites* habitats.

Discussion

Shifts in the composition of habitat-forming species and consequences for the function of ecosystems pose new challenges for conservation as the composition of assemblages that rely on habitats for food and shelter reorganise [7,51]. Focusing on coral reefs, we show that the taxonomic and functional composition of herbivorous fish assemblages, and rates of browsing, but not grazing, differed among taxonomically distinct coral habitats. Browsing on the red macroalga *Laurencia* was greatest in soft coral and mixed coral habitats, and lowest in branching *Porites* habitats. These differences in the consumption of *Laurencia* were best predicted by variation in both the composition and cover of benthic assemblages, with the highest rates of removal in habitats with the lowest coral cover, lowest structural complexity, and highest cover of dead substrata and macroalgae. Interestingly, rates of browsing on *Laurencia* were poorly reflected by visual estimates of the biomass of browsing fishes,

343 despite browsing fishes being recorded in all three habitats. In contrast to browsing rates,
344 grazing on algal turfs did not differ among habitats. This contrast highlights that different
345 environmental mechanisms, such as those determined by the influence of differential habitat
346 characteristics on foraging behaviour, may shape the functional impact of key species and
347 functional groups such that shifts in species configurations under mounting disturbances may
348 have varied consequences for maintained ecosystem function [7,8].
349
350 Observed variation in rates of browsing among habitats was best predicted by the cover and
351 composition of benthic communities, indicating that particular habitat characteristics may
352 influence foraging behaviour and/or habitat selection by browsing reef fishes. The cover of
353 live coral and structural complexity of reef habitats typically have positive effects on the
354 abundance, biomass, and diversity of herbivorous fish communities [33,52], and rates of
355 herbivory [35,36]. In contrast, however, we found that browsing on *Laurencia* was greater in
356 habitats with lower coral cover that had lower structural complexity, and higher cover of dead
357 substrata and macroalgae (e.g. mostly mixed coral habitats, largely characterised by massive
358 and branching *Porites*, *Sarcophyton*, *Lobophyton*). Conversely, whilst branching *Porites*
359 habitats were the most structurally complex [22], had the highest coral cover, and the greatest
360 observed biomass of browsing fishes among habitats, no significant reduction in *Laurencia*
361 biomass was detected over a 24 h period. The negative relationship between the cover of
362 structurally complex corals (and conversely the positive relationship with the cover of dead
363 substrata and macroalgae) and browsing rates may be related to increased levels of visual
364 occlusion during feeding in high-relief habitats and hence greater risk of foraging [53,54].
365 Studies show the physical topography of structurally complex habitats can inhibit access to
366 algal resources at fine scales (i.e. between coral branches [55]), and can alter the foraging
367 behaviour of fishes by reducing their visual fields and thereby enhancing perceived predation

risk [53]. Such findings reflect patterns of habitat use in other terrestrial and aquatic systems where foraging species favour open over structurally complex habitats due to the enhanced ability to detect approaching predators (e.g. African savannahs: [56,57]; temperate intertidal rocky shores and mudflats: [58]; alpine forests: [59]; European grasslands: [60]; temperate arable areas: [61]). Indeed, evidence shows that visual obstruction can increase vigilant predator-scanning behaviour at the cost of time spent foraging in various taxa [57,60]. Moreover, perceived predation risk can also be mediated by body-size with larger prey less susceptible to predation [56]. Of the four main species recorded feeding on *Laurencia* in our study, only *Pomacanthus sexstriatus* was observed feeding within the structurally complex branching *Porites* habitat, despite *Naso brevirostris* and *Siganus doliatus* being recorded in visual surveys of that habitat. *P. sexstriatus* was the largest-bodied species observed (mean biomass ± SE: 670 g ± 77; other species mean biomass 195-539 g), potentially reducing predation risk and enabling less discriminant foraging activity.

The positive relatitionship between browsing and the cover of dead substrata and macroalgae (which was highly collinear with the cover of live coral), also suggests that habitat condition may influence the foraging behaviour of herbivore fishes. Indeed, feeding rates by herbivorous reef fishes can be higher in degraded areas, of often lower topographic complexity [37]. By feeding where food resources are more abundant, animals may maximise net energy gain by reducing energetic costs of movement [62,63], and risk of predation associated with moving larger distances between resource patches [64]. In our study, differential browing rates may relate to the differential availability of algal dietary resources [35,39] following the bleaching event that caused coral loss and increased the cover of turf algae (Fig. 1a; [6]) at our study sites (between 52.4-71.4% cover of dead substrata). Browsing on *Laurencia* was greatest in mixed coral habitats that also had the highest cover of dead

substrata and macroalgae as a result of the bleaching (due to loss of mainly *Acropora* and soft coral taxa; [6]), and highest biomass and diversity of herbivorous fish. Increased cover of algae (predominately turf communities) following large-scale bleaching-induced coral mortality and subsequent increases in the abundance and/or biomass of herbivorous fishes (e.g. [65]), has led to suggestions that herbivorous fish populations may be food limited in areas of high coral cover [66]. However, this relationship may not hold at very low levels of macroalgal cover [34], such as those observed in the present study (mean: 0.3-1.4% cover).

While visual census estimates show macroalgal browsing herbivores are present in each of the studied habitats, browser biomass was a poor predictor of browsing rates. This is consistent with previous studies of herbivorous coral reef fishes [36,50] and processes in other systems (e.g. the decomposition of dung by invertebrates: [67]; pollination by bees: [13]) in which abundance shows little relation to their functional impact. The discrepancy between observed browser presence and function in our study may also reflect the high mobility and opportunistic foraging behaviour of roving herbivores [68], or the diver-negative behaviours of some fishes [69]. The utility of using the density or biomass of browsing herbivores as a proxy for macroalgal removal may be further hindered by the plasticity and opportunistic diets among herbivorous fishes [47], and a potential bias in the literature classifying browsers as those species known to feed on large fleshy brown macroalgae versus those that consume other fleshy macroalgae [48].

In contrast to browsing, there were no detectable differences in grazing on the algal turf assays among habitats. This provides further evidence of a disconnect between the observed density and realised impact of functional groups of herbivorous fishes. Despite no detectable differences in grazing rates, among habitat differences in herbivore assemblages were largely

418 driven by differences in the biomass of grazing species. The lack of among-habitat variation
419 in grazing may be related to the high diversity of fishes that feed on algal-turf covered
420 substrata [41], and their response diversity to changes in benthic composition [70]. Similarly,
421 the lack of observed differences may be due to grazing herbivores preferentially targeting
422 sparse and short early-successional turfs and avoiding later successional dense turf
423 assemblages [71]. Feeding rates and foraging behaviours of grazing coral reef fish species
424 have been shown to vary with the condition and structure of reef habitats and algal
425 communities, however responses tend to be species specific [37]. The among-habitat
426 variation in the changes in the turf height on caged tiles was interesting as, despite feeding by
427 large herbivorous fishes being excluded, there was a decline in height in soft coral habitat and
428 increase in branching *Porites* habitat which may be related to grazing by small invertebrates
429 and/or differences in algal productivity [72]. Similarly, negative values of turf height loss for
430 both caged and exposed assays in branching *Porites* habitats may be due to high algal
431 productivity in that habitat, warranting further investigation.
432
433 Our results provide new evidence of the variable influence of the composition and cover of
434 habitat-building corals on two key functions on coral reefs—grazing and browsing—based on
435 comparisons among three taxonomically distinct coral habitats. While the use of *Laurencia*
436 has provided valuable information on the variable browsing behaviour among habitats,
437 previous studies have shown rates of macroalgal browsing can be dependent on the
438 macroalgae used due to feeding preferences of local herbivore assemblages [48,49].
439 Therefore, further investigation using other commonly occurring macroalgae may offer
440 insight into behavioural variation among habitats of a broader suite of herbivores. Similarly,
441 herbivory processes can vary with depth, exposure, and reef zonation [33,73,74]. Our study
442 compared relatively small experimental assay units among habitats within in a sheltered

443 lagoon environment. Therefore, further study across a wider range of environmental
444 gradients, reef zones, across additional coral species configurations, and across broader
445 spatial scales is now needed. Our study coincided with a large-scale bleaching event [44],
446 resulting in rapid coral loss and changes in reef fish assemblage structure among our study
447 sites [6], and likely affected the foraging behaviour of a range of reef fish species including
448 herbivores [15,65,75]. Although the present study provides clear evidence of how herbivory
449 processes can vary with coral species composition, it was carried out in the context of this
450 disturbance. Disturbance dynamics are complex [15,70], and it is likely that fish assemblages
451 are in transition with changes in coral cover. Further research into the spatio-temporal
452 variation in foraging behaviour of individuals and functional groups across such disturbances
453 would improve our understanding of how changing reef configurations interact with climate
454 change impacts to influence critical ecological functions [15,16].
455
456 Understanding causal links between habitat species composition and ecosystem function is of
457 growing concern in this era of unprecedented and rapid ecological change [5,7,9]. In
458 particular, elucidating how the increasing modification of ecological communities affects
459 ecosystem processes is central to our capacity to anticipate whether new species
460 configurations will continue to provide goods and services as required by societies that
461 depend on them [14,17,23]. On coral reefs, whether herbivores can compensate for increased
462 algal production as coral cover decreases, and maintain critical rates of algal consumption
463 will be fundamental to the persistence of reconfigured coral-dominated systems [66]. Our
464 results show that herbivore assemblage structure varied among the studied habitats, however
465 did not reflect the observed variation in herbivory rates. While grazing was insensitive to
466 variation in coral composition, browsing varied considerably, indicating that different
467 mechanisms determined by specific habitat characteristics may be shaping these key

processes. While the precise mechanisms are not known, variation in browsing was best predicted by the composition and cover of benthic communities, and conversely the cover of dead substrata and macroalgae, characteristics that underscore the structural complexity of reef habitats and which may have influenced differential foraging behaviour. With ongoing degradation of coral reefs and the homogenization of both coral and fish assemblages [6,20], these results suggest that, within reefs, key ecosystem functions will likely vary among altered coral configurations, according to the differential vulnerability of corals to disturbances and ecological interactions between reef fishes and their environment [15]. More generally, our results emphasise the role of differential habitat characteristics and provide explicit support for assigning greater concern to the composition and structure—as well as cover—of habitat-building species in assessments and management of ecosystem function [7,23].

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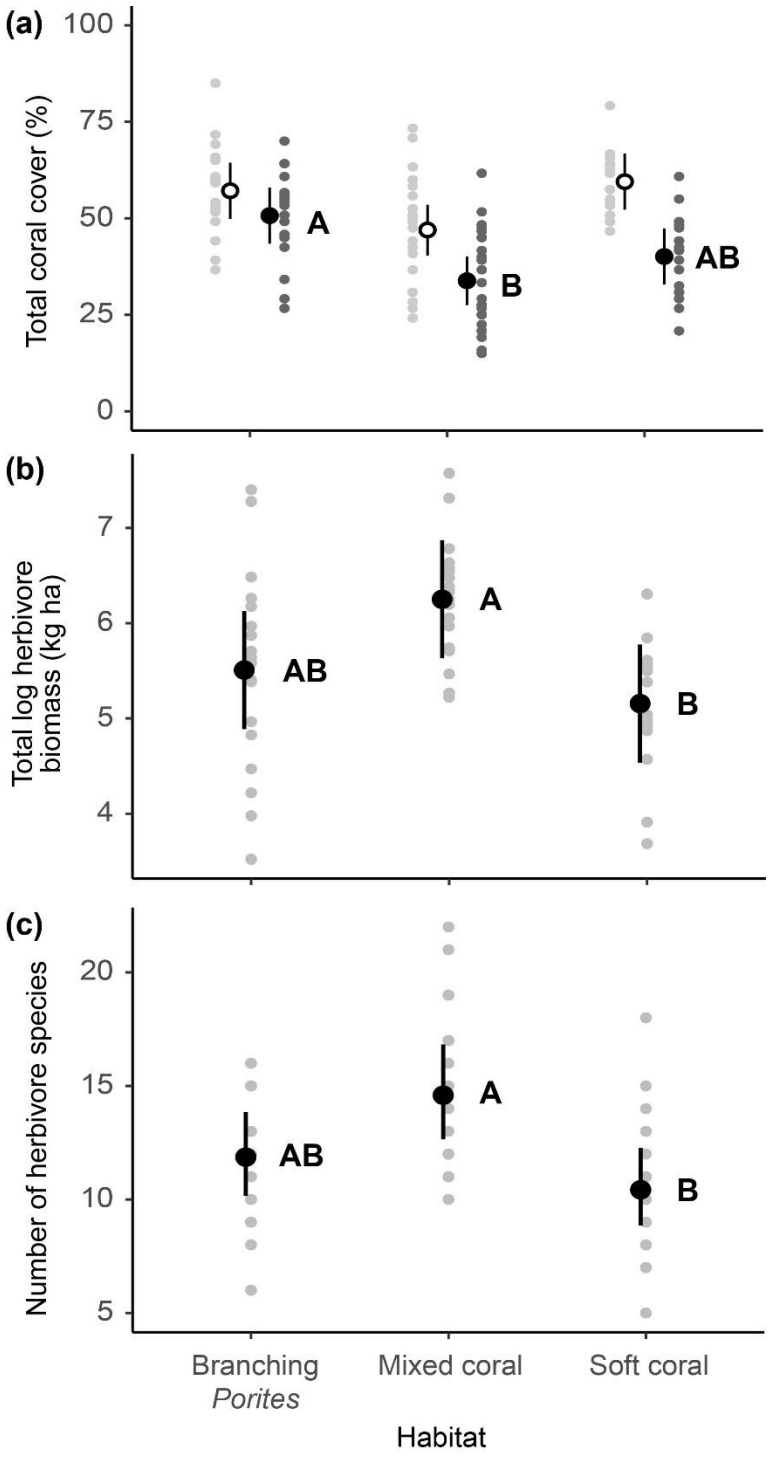
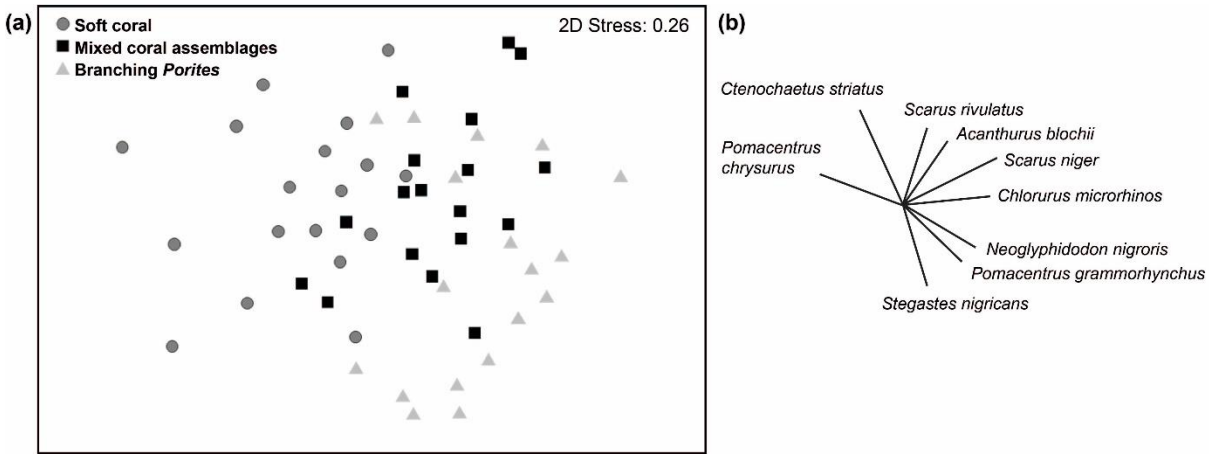


705

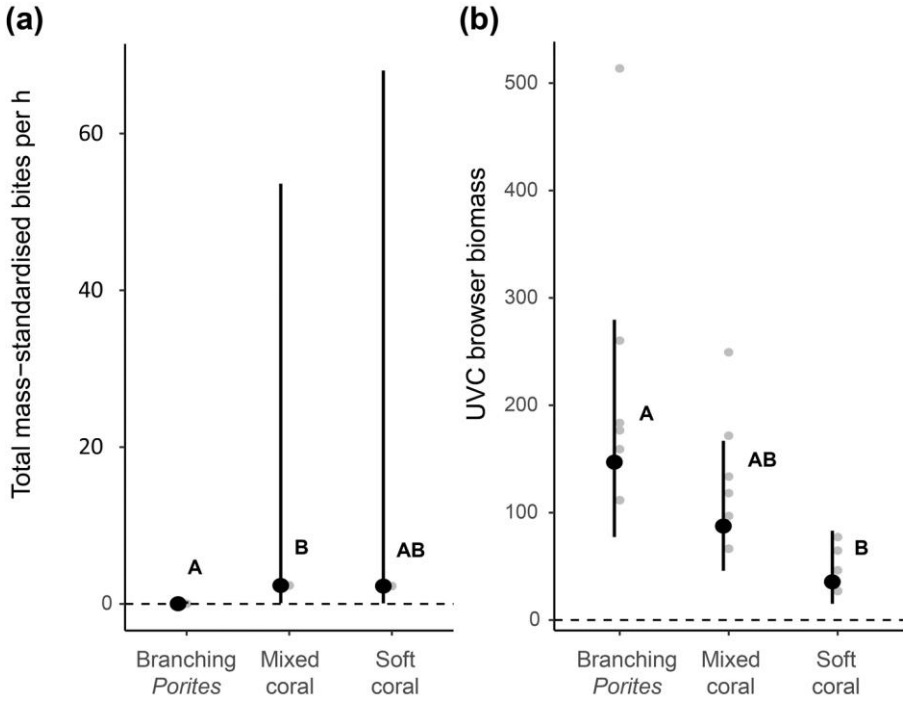
706 **Fig. 1** Among-habitat variation (fitted values ± 95% confidence intervals) in, (a) total coral
707 cover (hard and soft coral) in September 2015 (white; [6]), and April 2016 (black); (b) total
708 herbivore biomass (log-transformed, kg ha^{-1}); (c) number of herbivore species. Partial residuals
709 in grey; contrasting letters indicate significant differences among habitats (Tukey, $P<0.05$).



710

711 **Fig. 2** Non-metric multidimensional scaling analysis showing variation in taxonomic
712 composition of herbivorous fishes among surveyed coral habitats, using transect-level log
713 (x+1) transformed data (a). The relative contribution of species to the observed variation in
714 composition (>0.5 Pearson correlation) (b)**.**

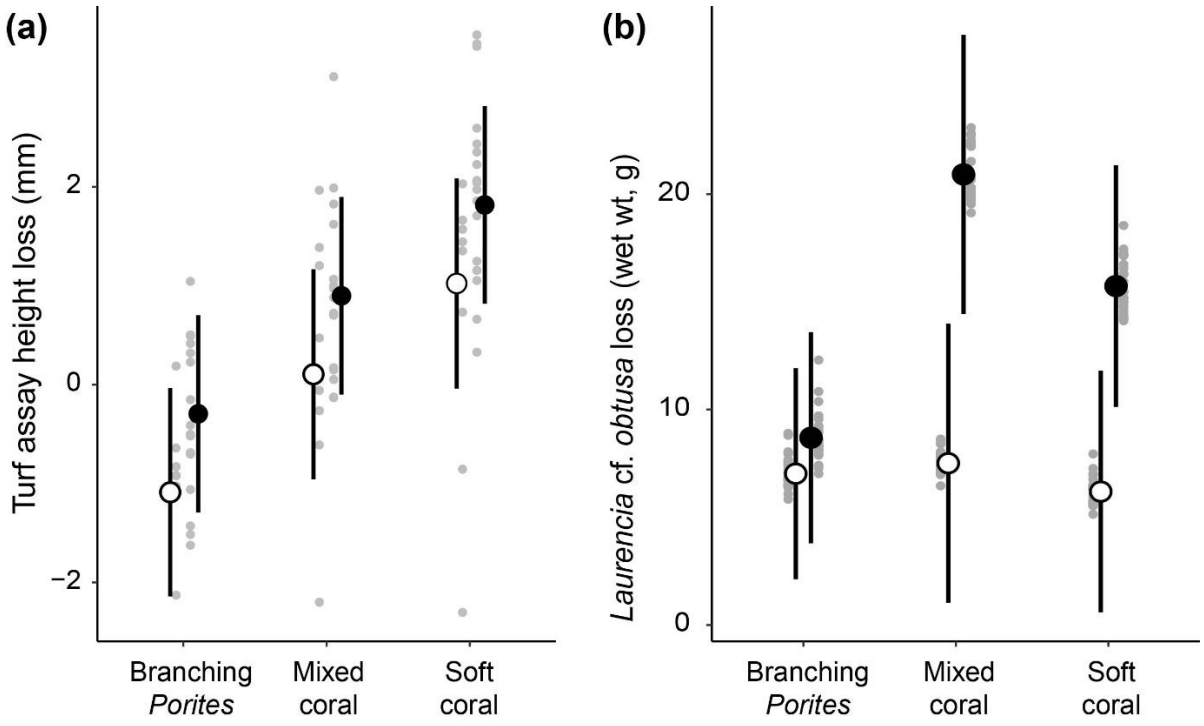
715



716

717 **Fig. 3** Among-habitat variation (fitted values ± 95% confidence intervals) in: (a) feeding rates
718 on *Laurencia* assays by all species; (b) visual biomass estimate of all nominal browsers (kg ha^{-1}).
719 Contrasting letters indicate significant differences among habitats (Tukey, $P<0.05$).

720



721

722 **Fig. 4** Among-habitat variation (fitted values ± 95% confidence intervals) in assay loss of: (a)
723 turf algae (mean turf height (mm); (b) *Laurencia* (wet weight, g); caged assays (white), exposed
724 assays (black); partial residuals (grey).